UNDERSTORY VEGETATION IN FULLY STOCKED PINYON-JUNIPER STANDS

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Abstract.— Ten fully stocked pinyon-juniper stands contained a total of 73 species in the understory, but the number of understory species in any one stand was moderately low ($\bar{x}$ = 20). On each stand, species of at least five different plant groups were present in the understory (shrub, perennial grass, perennial forb, annual grass, or annual forb). A perennial grass, Sandberg bluegrass (*Poa sandbergii*), and a group of annual forbs with relatively high cover and constancy among stands appeared best adapted to coexist with the pinyon-juniper overstory. The proportion of total plant cover was greater on tree-associated microsites (duff and transition) than in the interspace between trees because of the greater surface area of the former in most stands. The transition microsite was the most favorable for understory species and provided understory cover in disproportionately greater amounts than the area it occupied.

In the sampled stands, the majority of available resources was apparently utilized by the tree species (fully stocked), and only a sparse understory existed. Understory species are of little import to total biomass within fully stocked stands of singleleaf pinyon pine (*Pinus monophylla*) and Utah juniper (*Juniperus osteosperma*), but they represent the only available forage and the species most likely to reclaim the site following disturbance. Numerous small annual forbs and/or scattered suppressed perennial species characterize the sparse understory. A meaningful characterization of the amount and distribution of individual understory species is made difficult by the ephemeral nature of annuals and the patchiness of understory within the stands.

Distribution of understory is not uniform among soil microsites in these woodlands or in other forest situations because of overstory effects on shading, rain interception, and dense duff layers (Anderson et al. 1969). Less visible differences among soil microsites, such as nutrient concentration under the crown and its depletion in interspace zones (Zinke 1962, Barth 1980) and ameliorated microclimate under tree crowns (Johnsen 1962), also effect understory distribution.

The soil surface within fully stocked pinyon-juniper stands can be characterized as a mosaic of duff under the crown, a transition zone of scattered needles surrounding the duff, and bare ground between trees. We defined duff as a soil microsite with 90 percent or more ground surface covered by needles to a depth greater than 0.5 cm. Transition microsites are defined as having 20–90 percent of the soil surface covered by needles with an average depth of less than 0.5 cm. Interspace microsites are characterized by less than 20 percent needle cover of less than 0.5 cm depth.

It is not the purpose of this study to illuminate characteristics of specific microsites that control understory plant distribution, but to record differences in plant cover between duff and transition microsites and between mean plant cover of these tree-associated microsites and that of interspace. We used the proportion of total plant cover provided by each microsite in a stand and plant cover/m^2 of each microsite to illuminate these differences.

Methods

Ten fully stocked stands were sampled for understory species cover and distribution in 1978 (Fig. 1). Observations reflect only a "snapshot" view of the understory vegetation. Subsequent sampling was impossible because trees were soon harvested. At each stand, a square plot 30 m to a side was established. Five line transects 20 m in length were laid out at 5-m intervals parallel to each other across the slope. Tree cover was estimated by line intercept. A 50 × 50 cm

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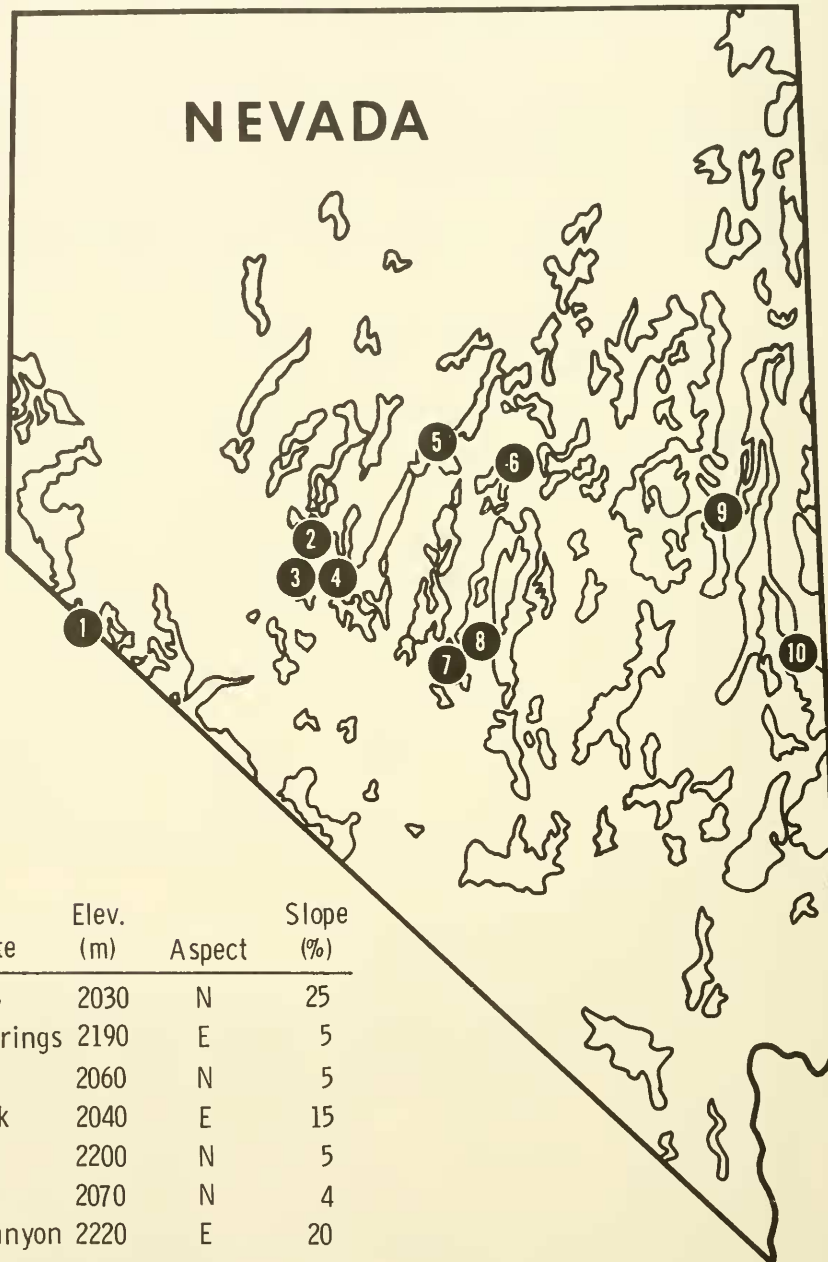
frame was laid down at every meter mark along the transects, and understory species cover, density, and type of soil microsite were recorded for each frame. Results were used to estimate plant cover distribution among soil microsites across the entire stand. As sampled microsites along the transect are disjunct and subject to wide variations in



No.	Study Site	Elev. (m)	Aspect	Slope (%)
1	Fredricks	2030	N	25
2	Camel Springs	2190	E	5
3	Ridge	2060	N	5
4	Paperback	2040	E	15
5	Austin	2200	N	5
6	Monitor	2070	N	4
7	House Canyon	2220	E	20
8	Willow Creek	1070	W	3
9	Lowry Springs	2200	N	17
10	Mt. Wilson	2200	E	3

Fig. 1. Location of study sites in relation to pinyon-juniper woodlands of Nevada. Woodland distribution patterns taken from Pinyon-Juniper woodlands of the Great Basin (Tueller et al. 1979).

microclimate, another set of contiguous transects was used to compare differences in plant cover/m² of each microsite.

Four pairs of trees were selected for tree-to-tree transects. Each tree was at least 20 cm in diameter, and trees of each pair had at least 1 m of interspace between them. A series of 50 × 50 cm frames was laid contiguously the entire length of these transects from tree bole to tree bole. It was hoped contiguous frames reduced microclimate variability among microsites and served to eliminate understory variability due to inclusions of remnants from the past shrub-dominated community. Plant cover and soil microsite type within each frame were recorded. Data were converted to plant cover/m² of each soil microsite, and this was used as a crude estimate of microsite favorableness for understory species.

TABLE 1. Constancy and relative importance values for understory species.

Species[1]	Constancy[2]	Relative importance values[3]	Species	Constancy	Relative importance values
	percent			*percent*	
Grass (grasslike)			Shrubs		
Poa sandbergii	90	100.0	*Phlox hoodii*	80	5.7
Sitanion hystrix	80	5.2	*Artemisia tridentata*		
Bromus tectorum	40	1.5	spp. *vaseyana*	40	13.3
Stipa thurberiana	20	—[4]	*Purshia tridentata*	40	3.5
Agropyron spicatum	10	1.2	*Leptodactylon pungens*	20	0.2
Carex sp.	10	—	*Artemisia arbuscula*	10	0.5
Oryzopsis hymenoides	10	0.1	*Artemisia tridentata*		
Stipa pinetorum	10	0.01	spp. *wyomingensis*	10	3.3
			Cercocarpus ledifolius	10	—
Perennial forbs			*Ephedra viridis*	10	0.2
Arabis holboellii	90	1.6	*Eriogonum caespitosum*	10	—
Astragalus purshii	60	0.5	*Eriogonum microthecum*		
Astragalus iodanthus	30	0.3	var. *lapidicola*	10	—
Phlox stansburyi	30	0.1	*Eriogonum umbellatum*		
Cymopterus watsoni	20	0.1	var. *juniporinum*	10	—
Erigeron caespitosus	20	0.2	*Ribes velutinum*	10	—
Lomatium macrocarpum	20	0.4			
Lomatium nevadense	20	—	Annual forbs		
Lupinus sp.	20	—	*Gilia brecciarum*	80	11.8
Senecio multilobatus	20	0.1	*Collinsia parviflora*	70	7.7
Agoseris glauca	10	0.1	*Cryptantha watsonii*	60	0.9
Allium atrorubens	10	0.1	*Gayophytum ramosissimum*	60	3.7
Antennaria rosea	10	—	*Microsteris gracilis*	60	11.9
Arenaria kingii	10	—	*Mentzelia albicaulis*	50	0.5
Astragalus sp.	10	—	*Eriastrum sparsiflorum*	50	0.1
Astragalus calysosus	10	—	*Polygonum douglasii*	50	0.5
Astragalus filipes	10	—	*Gayophytum nuttallii*	40	0.8
Calochortus nuttallii	10	—	*Gilia tennerrima*	40	3.2
Comandra pallida	10	—	*Gilia violaceum*	30	0.9
Cordylanthus kingii	10	—	*Cryptantha torreyana*	30	0.7
Crepis occidentalis	10	—	*Descurainia richardsonii*	30	0.1
Cryptantha flavoculata	10	0.2	*Linanthus septentrionalis*	30	0.6
Erigeron argentatus	10	—	*Navarretia breweri*	30	0.1
Haplopappus acaulis	10	—	*Chenopodium album*	10	—
Ipomopsis congesta	10	0.1	*Calytonia perfoliata*	10	—
Lithophragma bulbifera	10	—	*Collomia grandiflora*	10	—
Pedicularis crenulata	10	—	*Epilobium paniculatum*	10	—
Penstemon eatoni	10	—	*Erigonum vimineum*	10	—
Penstemon kingii	10	—	*Galium bifolium*	10	—
Penstemon speciosus	10	0.5	*Phacelia affinis*	10	—
Streptanthus cordatus	10	—	*Phacelia humilis*	10	5.2

[1]Species nomenclature from Holmgren and Reveal (1966).
[2]Constancy: number of stands where species occurs/total number of stands.
[3]Importance values: species total percent cover · constancy. Relative importance value (*RIV*): (species importance value/max importance values)·100.
[4]*RIV* <0.1 not shown.

Individual species cover within the understory was so sporadic that species data had to be combined and transformed (log $[x + 1]$ or arcsine $\sqrt{\%}$) to effectively reduce skewness and kurtosis. Plant data were grouped into totals for perennial and annual species before running in a two-way factorial analysis with the second factor, soil microsites (duff, transition, interspace). Data from each site were analyzed separately, using transects as replicates. Differences in the proportion of total plant cover and plant cover/m^2 of microsite between duff and transition soil microsites and between their mean value and that of interspace were compared in a series of completely orthogonal contrasts. Orthogonal contrasts are generally viewed as stronger statistical tests than the more commonly used multiple range tests, but are limited in that fewer treatments can be tested and all treatments tested must be orthogonal to each other. Proportion of total plant cover by soil microsite was used to show distribution of plant cover among microsites without compensating for differences in area. Plant cover/m^2 was used to show relative "favorableness" of a microsite for understory on a per unit basis.

Results and Discussion

STAND CHARACTERIZATION.— The junior author identified a total of 73 understory taxa in the sampled stands (Table 1). As our study was limited to only pinyon-juniper stands in late succession stages and correspondingly high tree cover (Table 2), we found fewer understory species than previously reported for pinyon-juniper woodland of the Great Basin (Tueller et al. 1979). Rabbitbrush (*Chrysothamnus* sp.) species were notably absent from our sites, but annual forbs, little blue-eyed Mary's (*Collinsia parviflora*), borage (*Cryptantha* sp.), and the perennial grass, Sandberg bluegrass, had much higher constancy values than were previously reported by the above authors. We tentatively suggest rabbitbrush disappears more rapidly than other shrubs as pinyon-juniper competition increases, and annual forbs increase. Long-term successional studies are required to test this idea.

Perennial forbs had the greatest number of species (31) among stands. Next in order were annual forbs (23), shrubs (11), perennial grass (7), and annual grass (1) (Table 1). Although perennial forb species were numerous, they were not ubiquitous. Only 32 percent of the perennial forbs were found on more than one stand, as compared with 70 percent of the annual forbs, 73 percent of the shrubs, and 57 percent of the perennial grass. The range of constancy values, 10–90 percent (Table 1), reflect the variability in individual species occurrence among stands. The annual forb plant form class had the greatest number of species with ≥50 percent constancy values.

A relative importance value (*RIV*) was used to indicate the relative importance of a species in providing understory cover in sampled stands (Table 1).

Importance value (*IV*) = constance · percent cover (sum of all stands)

Relative importance value (*RIV*) = (species *IV*/ max *IV* [all species]) · 100

We found important understory species (*RIV* ≥5) to be Sandberg bluegrass, squirrel-tail (*Sitanion hystrix*), phlox (*Phlox hoodii*), big sagebrush (*Artemisia tridentata*), microsteris (*Microsteris gracilis*), gilia (*Gilia brecciarum*), blue-eyed Mary's, phacelia (*Phacelia humilis*).

TABLE 2. Percent tree cover on the 10 study sites.

	Study site									
	Mt. Wilson	Monitor	Fred-ricks	House Canyon	Willow Creek	Camel Springs[1]	Ridge[1]	Paper-back	Austin	Lowry Springs
Tree species:										
Pinus monophylla	52	63	36	13.4	38	58	52	56	29	30
Juniperus osteosperma	4			12.3	3				14	20
Total cover	56	63	36	25.7	41	58	52	56	43	50

[1]Cover values from Meeuwig (1979).

Table 3. Number of species by plant group.

Plant form	Site											
	Mt. Wilson	Monitor	Fredricks	House Canyon	Willow Creek	Camel Springs	Ridge	Paperback	Austin	Lowry Springs	$\bar{x}$	CV[1]
												(%)
Shrubs	0	1	2	4	5	3	3	3	3	4	2.8	50
Perennial												
Grass	1	2	2	2	3	2	2	3	2	6	2.5	51
Forb	2	1	0	8	6	2	5	6	6	18	5.4	90
Annual												
Grass	1	0	1	0	0	1	1	1	0	0	0.5	100
Forb	3	8	12	9	8	10	10	15	8	2	8.5	43
Total	7	12	17	23	22	18	21	28	19	30	19.7	33

[1]CV (%): coefficient of variation = $\left(\frac{\text{Standard deviation}}{\text{Mean}}\right) \times 100$.

Sandberg bluegrass was by far the most important structural component of the understory. All perennial forbs had low relative importance values because of low cover values.

Number of understory species occurring on a single site varied from seven to 30 among sites with a mean of approximately 20 species (Table 3). Total number of understory species at each site varied less (coefficient of variation [*CV*] = 33 percent) than species numbers in individual plant groups among stands (Table 3). At least four plant groups were represented at each stand. Annual forbs had the greatest number of species on all sites except Lowry Springs. Annual forbs also had the least variability of the plant forms in species numbers among stands (*CV* = 43 percent). The predominance of annual species is characteristic of pinyon-juniper woodlands here and in New Mexico, but in Utah perennial forbs predominate (Harner and Harper 1976) (Table 4). Low variability in the relatively large number of annual forb species among stands indicate annual forbs have adapted to utilize the limited resources available within fully stocked stands; but because of the ephemeral nature of annuals they utilize these resources on an intermittent basis. A diversity of plant groups at each stand also suggested that, although limited, resources available under the intense tree competition can still meet the demands of physiologically different species.

Understory cover was low ($\bar{x}$ = 3.4 percent) with a high coefficient of variation (*CV* = 60 percent) among stands (Table 5). Cover values ranged from 0.02 percent at Mt. Wilson to 7.19 percent at Fredricks. These values are low, but are probably an overestimate of "normal" understory cover; 1978 was a wetter year than "average" on many sites. St. Andre et al. (1965) reported similar low cover values ($\bar{x}$ = 2.65 percent) for herbaceous understory in the pinyon woodland of the White Mountains in California.

No one plant form class had the greatest proportion of cover on all sampled stands, but annual forbs and perennial grass consistently made up a large portion of the understory cover (Table 5). There were high coefficients of variation in the proportion ($_p$) of total plant cover for plant group classes

Table 4. Mean percent of species contributed by plant group.

	Shrub	Perennial		Annual	
		Grass	Forb	Grass	Forb
Nevada	14.2	12.6	27.4	2.7	43.1
Utah[1]	18.8	17.0	39.8	24.4	
New Mexico[1]	24.9	13.5	24.4	37.2	

[1]From Harner and Harper (1976).

among stands, but less variation among annual forb and perennial grass classes. Results suggest that the perennial grass, Sandberg bluegrass, and annual forbs are well adapted to coexist within fully stocked pinyon and juniper stands.

SOIL MICROSITES AND PLANT GROWTH.— The duff microsite occurred more often in transects and correspondingly occupied a greater proportion of the ground surface than the transition microsite on all stands (Table 6). Contrary to expectations, the proportion of understory on the transition microsites exceeded that of duff on five of nine sites tested (Table 7). This anomaly and lack of significant differences in the proportion of understory cover between duff and transition microsites on seven of nine sites suggests both microsites provide a similar amount of understory cover, but cover provided by transition microsites is disproportionately greater than the surface area it occupies.

This supposition was substantiated by greater plant cover/m² (Table 8) in transition than duff microsites in tree-to-tree transects in seven of the nine sites. This relationship was significant at Austin, Willow Creek, Ridge, Paperback, and Monitor. Only at Fredricks, where duff was shallow and the understory dominated by the annual forb phacelia (*Phacelia humilis*), did duff plant cover/m² significantly exceed that of transition microsites. The close association of *Phacelia vallismortae* with pinyon trees has been previously reported by St. Andre et al. (1965).

The completely orthogonal contrast procedure prohibited the direct comparison of plant cover on transition and interspace microsites, but transition microsites had greater proportion of total plant cover and greater plant cover/m² than interspace at seven of nine sites as indicated by values in Tables 7 and 8. Differences in plant cover/m² between transition and interspace indicate the favorableness of the transition microsite for understory growth and are not the result of differences in numbers of each microsite sampled.

Duff and transition microsites combined exceeded interspace in total number and corresponding surface area in all stands except Willow Creek and House Canyon (Table 6). The total proportion of plant cover provided by duff plus transition microsites greatly exceeded the proportion of plant cover on interspace microsites at all stands but Willow Creek and Lowry Springs (Table 7).

We could not determine significant differences ($p \geq 0.1$) in proportion of understory cover between interspace microsites and the mean of tree-associated microsites (duff + transition/2) at six of nine stands (Table 7). At Fredricks and Paperback mean understory cover on tree-associated microsites was significantly greater than the interspace, but the

TABLE 5. Proportion (π) of total plant cover by plant group class and total plant cover (%) among stands.[1]

Site	Shrub π (%)[2]	Perennials: Grass π (%)	Perennials: Forb π (%)	Annuals: Grass π (%)	Annuals: Forb π (%)	Total plant cover (%)[3]
Mt. Wilson	–	4.2	4.2	4.2	87.5	0.02
Fredricks	–	–	–	–	100.0	7.18
House Canyon	17.6	9.7	4.6	–	68.1	1.64
Willow Creek	95.8	0.7	0.1	–	3.4	4.44
Camel Springs	29.9	36.7	4.1	–	29.3	3.38
Paperback	18.8	49.1	2.1	6.1	23.9	5.58
Monitor	2.9	71.6	2.1	–	23.3	1.39
Austin	0.8	74.5	4.0	–	20.7	2.46
Ridge	5.2	83.0	1.3	0.4	10.1	4.92
Lowry Springs	9.0	53.7	37.2	–	–	3.11
$\bar{x}$	18.0	38.3	6.0	1.1	36.6	3.42
CV (%)[4]	153	81	176	194	92	60

[1]Data from the five parallel transects.
[2]Proportion ($_p$) of the total plant cover provided by each plant form in percent.
[3]Percent cover: total plant cover as percent of ground surface it covers.
[4]CV (%): coefficient of variation = $\left(\frac{\text{Standard deviation}}{\text{Mean}}\right) \times 100$.

TABLE 6. Number of frames[1] identified as duff, transition, or interspace microsites.[2]

	Site									
Microsite	Mt. Wilson[3]	Monitor	Fred-ricks	House Canyon	Willow Creek	Camel Springs	Ridge	Paper-back	Austin	Lowry Springs
Duff (D)	33 (55)	43	52	34	31	44	54	46	57	53
Transition (T)	18 (30)	42	24	15	11	30	28	27	16	20
Interspace (I)	9 (15)	15	24	51	58	26	18	27	27	27

[1]Number of frames equates to percent ground surface occupied by the microsite.
[2]Data from the five parallel site transects (100 total frames).
[3]Two transects at Mt. Wilson were deemed unusable due to large differences in tree ages from the major portion of the stand; thus percent ground surface occupied by each microsite is in parentheses.

opposite occurred at Willow Creek. Cover differences are due to microsite "favorableness" at Fredricks, as indicated by greater plant cover/m^2 on tree-associated microsites (Table 8). At Willow Creek and Paperback differences in proportion of plant cover are due to differences in surface areas of the microsites.

The lack of significant differences in proportion of plant cover and plant cover/m^2 on tree-associated microsites versus interspace suggests overall favorableness of tree-associated microsites is not different from that of interspace on most sites. The presence of tree root competition in all microsite types of fully stocked stands (Woodbury 1947 and our own observations) would tend to lower production on all microsites and ameliorate differences. This hypothesis is in variance with previous reports of increasing understory production under tree crowns of alligator juniper (*Juniperus deppeana*) (Clary and Morrison 1973) and apparently an increase in production with distance from the stem of one-seeded juniper (*Juniperus monosperma*) (Arnold 1964).

PERENNIAL AND ANNUAL PLANT COVER.— Proportion of understory cover provided by annuals and perennials varied greatly among stands. Understory at Mt. Wilson, Fredricks, and House Canyon was dominated by annual forbs, but perennials (shrubs and grass) dominated the understory on the remaining stands (Table 7). Both annuals and perennials are adapted to coexist with the overstory species. The majority of species (excluding shrubs), either perennial or annual, complete growth early in the growing season before surface soils become dry (unpublished data).

INDIVIDUAL SPECIES.— Sandberg bluegrass was found to have greater cover in transition microsites than duff or interspace on five stands where it dominated the understory (data not shown). Plant density was also greater in the transition microsite, but not significantly so. Arizona fescue (*Festuca arizonica*) was reported to have a similar distribution pattern in a pinyon-juniper community in Arizona (Merkle 1952).

Other understory species occurred too infrequently within individual frames to be analyzed parametrically, but did appear to favor one microsite over another. *Cryptantha* species occurred more often in the duff microsites than elsewhere.

TABLE 7. Orthogonal comparisons of the proportion of total understory cover among soil microsites and perennial and annual species.[1]

	Site									
Orthogonal comparisons	Mt. Wilson[2]	Monitor	Fred-ricks	House Canyon	Willow Creek	Camel Springs	Ridge	Paper-back	Austin	Lowry Springs
D vs T[3]	—	16:64[4]	72:21	44:17	2:16	31:54	46:34	33:48	40:28	22:27
$\left(\frac{D+T}{2}\right)$ versus I	—	40:20	46:7	30:39	9:82	42:15	40:20	40:19	34:32	24:51
Perennials versus annuals	—	75:15	0:99°	32:68	96:04	70:30	89:11	72:28	77:23	100°:00

[1]Plant cover from the five parallel transects at each site.
[2]Understory cover at the Mt. Wilson site was so sparse as to prohibit parametric analysis.
[3]D = duff microsite, T = transition microsite, I = interspace microsite.
[4]═, ─, denotes significant difference at 0.05 and 0.1 levels, ° a biologically significant difference is assumed without statistical testing.

CONCLUSIONS

Numerous species and plant groups occur in the understory of fully stocked stands of pinyon and juniper, but numbers of species on any one stand are moderately low ($\bar{x}$ = 20) and they provide scant cover ($\bar{x}$ = ≤ 5 percent). A perennial grass, Sandberg bluegrass, and several annual forbs consistently provided the most understory cover among stands. Consistency in cover and a high number of species among stands indicated the annual forb plant group may be best adapted to coexist with the overstory species in fully stocked stands. The ephemeral nature of the annual forbs increases the year-to-year variability in understory cover and decreases the predictability of response if woodlands are disturbed. Management operations that remove tree cover should consider the scant understory in most stands and the potential erosion hazards.

Plant cover decreases in both directions from the transition microsite; thus response is at variance to previous reports of both decreasing and increasing cover toward the stem of pygmy forest tree species. The proportion of understory cover on duff and transition microsites is similar in most stands. Although duff occupied greater surface area, the transition microsite produced greater plant cover/m^2. Transition microsites appear more favorable for growth of understory species than those of duff or interspace. Tree-associated microsites provide more understory cover than interspace because they occupy a larger portion of the stand; they do not increase understory cover over that which could be expected from interspace.

Land managers should recognize that fully stocked pinyon-juniper woodlands are a composite of soil microsites that contain different proportions of the understory cover. These microsites may well respond differently to management practices; thus understory production will vary under the same management when proportions of the microsites vary.

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TABLE 8. Orthogonal comparison of the mean plant cover (dm)^2/m^2 occurring on each soil microsite.[1]

Orthogonal comparisons	Site									
	Mt. Wilson[2]	Monitor	Fred-ricks	House Canyon	Willow Creek	Camel Springs	Ridge	Paper-back	Austin	Lowry Springs
D vs T[3]		0.3:2.3[4]	10.3:5.4	3.2:3.1	0.6:7.4	1.6:4.6	2.8:8.5	3.7:8.3	0.8:4.7	2.2:3.7
$(\frac{D+T}{2})$ vs I	–	1.3:2.4	7.9:1.2	3.1:2.9	4.0:4.1	3.1:2.1	5.7:6.8	6.0:5.6	2.8:7.6	3.0:1.5

[1]Plant cover based on data from tree-to-tree transects.
[2]Understory cover at Mt. Wilson site.
[3]D = duff microsite; T = transition microsite; I = interspace microsite.
[4]═, — denotes significant difference at 0.05 and 0.1 levels.

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